Parr

The Reaction Of Pilobolus To Light.

THE REACTION OF PILOBOLUS TO LIGHT

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Rosalie Mary Parr

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BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF Doctor of Philosophy

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THE RESPONSE OF PILOBOLUS TO LIGHT

INTRODUCTION

Much work has been done on the response of organisms to light. Naturally all of the earlier and a large part of the later work was qualitative in nature. Up to the time of Wiesner's classic work on heliotropism, no attempt had been made to express the photic sensibility of plants in quantitative terms. Since the publication of his "Die heliotropische Erscheinungen im Pfanzen-reiche", ('79), little advance was made along quantitative lines until 1909, when Blaauw published "Die Perzeption des Lichtes". In this important contribution modern physical methods are for the first time employed. The conclusions of Blaauw, however, are not in agreement with those of Wiesner, and both contradict without adequate explanation, the results of the earlier investigators on phototropism, such as Gardner, Guillemin, Mueller, and others.

While considerable progress has been made in the study of the threshold of stimulation,- more especially as related to duration and intensity of the light stimulus,- we have no complete record of the response of a given organism to carefully graded and measured light energies in the different spectral regions.

A number of theories of response based on the interpretation of data obtained by experimental methods have been formulated and these shall be referred to as, I, Intensity difference; II, Ray direction; III, Wave-length; IV, Energy; V, Metabolism.

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I. THEORIES OF RESPONSE.

1. DeCandolle, (1832), the author of the "intensity"theory, believed that due to a difference in the light intensity upon the sides of the plant turned toward and away from the source of light, there results an increased carbon dioxide liberation and also an increased transpiration on the lighted side of the organism which brings about an earlier maturation of its cells and hardening of its tissues. Among the adherents to this theory, or to a more modern modification and interpretation of the same, may be mentioned Wiesner, ('79), Darwin, ('83), Oltmanns, ('92), Yerkes, ('03), Loeb, ('06), and Davenport, ('07).

Wiesner attributes the response to the difference in the lighting of the two sides coupled with the inhibiting action of light. He argues that if the organ were entirely transparent and no light were lost by reflection that heliotropic response would be impossible. He offers no experimental proof in support of this view because,as he says, of the difficulty in measuring the difference in light intensity of the two sides.

Charles and Francis Darwin, ('80), concluded that the difference in the intensity of the light on opposite sides of the plant modifies the nutation and results in the tropic movement.

Engelmann, ('83), found that a very gradual increase, or decrease, of light intensity produced no response in Caramecium bursaria. The same difference produced a response. He concluded that response follows a time rate of change of intensity.

Loeb, ('06), believes that because of the more intense

light on one side of the organism there is produced a difference in chemical constitution of the cells on the two sides which results in heliotropic action.

Oltmanns, ('92), by the use of India ink solutions in prismatic wedges attempted to show that the response of the organism is due to a difference of intensity rather than to direction of ray. A later paper, ('97), maintains that the intensity of the stimulus determines the direction - positive or negative - of the response of the organism.

2. Sachs, ('76), advanced the theory that the direction and degree of curvature is determined by the direction of the ray passing through the organism. The stimulus is perceived when the long axis of the organ forms an angle with the incident ray.

Strasburger, ('78), added substantial proof to the ray-direction theory. By the response of the swarm-spores of Botrydium and Bryopsis in a trough behind a prismatic wedge filled with a solution of humic acid variously placed with reference to the light source, he concluded that the directive stimulus is due to the direction of the impinging ray rather than to light intensity. Davenport and Canon, ('97), repeated the experiments of Strasburger, using a wedge-shaped container filled with India ink solution and found that the direction taken by Daphina was in the path of the light rays.

3. The relation between refrangibility and response was first attacked by Payer, (1842), who used colored glass screens spectroscopically tested. He found that cress seedlings behave in red, orange, yellow, and green as in total darkness, but respond positively in blue and violet, the blue being the more active.

Dutrochet, ('44), using similar screens found that cress seedlings failed to respond, but that other seedlings curve toward the red rays. His further experiments lead to the conclusion that response is not due to refrangibility but to the "brightness" of the light used.

The Italian botanist, Zantedeschi, (1843), showed that Oxalis multifloris responds to blue, violet, and green, but not to yellow, orange and red rays.

D. P. Gardner, ('44), studied the effect of the various regions of the sun's spectrum and concluded that rays of all refrangibility are capable of causing heliotropic response, but that the indigo rays had this property to the highest degree. He decided that the intensity of light had only a subordinate influence, since by increasing the intensity, the tropic response increased only slightly.

Guillemin, '58), exposed seedlings of cress and of mustard to the spectral regions obtained by passing the sun's rays through prisms of flint glass, of rock salt, and of quartz. His records show that heliotropic curvature is produced by the invisible chemical and heat rays, as well as by every region of the

[illegible]

visible spectrum, as had previously been stated by Dutrochet and Pouillet. He further found that the seedlings showed two maxima of response, one in the region between the violet and ultra-violet and the other between the infra-red and green. The positions of these maxima, however, shifted with a change of prisms, or with the position of the sun in the heavens, or with the water vapor in the air. The lower the position of the sun and the greater the amount of water vapor present in the air, the more the second maximum advanced into the visible regions. The more ready response in the violet which Dutrochet obtained, he explained as due to the absorption of the ultra-violet by the lenses used before the prism.

Sachs, ('64), using colored solutions found heliotropic response only in the blue end of the spectrum. He made no attempt to secure pure colors or to measure the intensity of the light emitted.

Wiesner, ('79), by the use of solutions determined that seedlings of Vicia curved in all regions of the visible spectrum excepting in the yellow, which he found to exert a retarding action upon the effect of orange and red rays when mixed with them. Using the sun's spectrum, he obtained practically the same results. In both series of tests he found a first maximum between violet and ultra-violet, and a second between the red and infra-red. The effect decreased from either end of the spectrum to zero in the yellow.

Dandeno, ('03), with glassfilters obtained results which

differ widely from those of the investigators already mentioned. He found a first maximum in yellow and a second in blue, with the minimum in green. His screens, when spectrosc c pically tested, did not give pure color.

Sorokin, ('73), Fischer von Waldheim, ('72), and Brefeld, ('81), studied the effect of light passed through a solution of potassium bi-chromate, and an ammoniacal solution of copper oxide, on Pilobolus reporting very different results. Thus, Sorokin claims that Pilobolus fails to grow in light filtered through the solution of copper oxide and that it gives a negative response to light filtered through potassium bi-chromate. Fischer von Waldheim obtained a strong positive response to the blue light while Brefeld had a positive reaction in both blue and red, especially strong in the red.

Table I.

Observer	Plant	Spectral Regions								
		Infra-red	Red	Orange	Yellow	Green	Blue	Indigo	Violet	Ultra-violet
Payer, ('42)	Cress	0	0	0	0	0	++	+	+	0
Zantedeschi, ('42)	Oxalis	0	0	0	0	+	+	+	+	0
Dutrochet, ('44)	Cress	0	0	0	0		+	+	+	0
Dutrochet, ('44)	Other Seedlings	0	+	+	+		+	+	+	0
Gardner, ('44)	Rape	0	+	+	+	+	+	+	+	0
Guillemin, ('58)	Cress	+	++	+	+	+	+	+	+	++
Sachs, ('64)	Mustard	0	0	0	0	+	+	+	+	+
Mueller, ('72)	Cress		+	+	+	+	+	+	+	
Sorokin, ('73)	Pilobolus		-	-	-		0	0	0	
Fischer von Woldheim, ('75)	Pilobolus		0	0	0		+	+	+	
Wiesner, ('79)	Vicia	+	+	+	-	+	+	+	++	+
Brefeld, ('81)	Pilobolus		+	+	+	+	+	+	+	
Graentz, ('98)	Pilobolus		+	+	+	+	+	+	+	+
Dandeno, ('03)	Seedlings	+	+	+	++	+	+	+	+	
Blaauw, ('09)	Phycomyces	0	0	0	+	+	+	++	+	+

The above summary shows the conflicting results obtained by a number of investigators on the response of plants to rays of light of different refrangibility.

The attempts to correlate the heliotropic response in plants with an energy value of the light appears first in the work of N. J. C. Mueller, ('72). While experimenting with cress seedlings in the objective spectrum, he found that the maximum shifted in repeated experiments and he concluded that the "mechanical intensity" varied for one and the same color. He believed that the blue-violet rays, because of their small intensity were absorbed in the cells of the lighted side, hindering growth on that side. The longer waves, because of their greater energy, penetrated the tissue more deeply, having equal effect on the two sides and no curvature resulted. He did not give further experimental proof of this theory.

Haberlandt, ('02), developed a very interesting theory of response. He considered the epidermal cells as small lenses which focus the light rays upon the sensitive protoplasmic membranes of the underlying cells. Maxwell and Lebedev showed that light exerts a pressure approximately equivalent to .4 mg. to the square meter of absorbing surface, and Haberlandt suggests that the response is due to the pressure exerted by the light in a way somewhat similar to the response of a tendril when stimulated by a pressure equal to a weight of .0002 mg.

Wager, ('09), modified Haberlandt's "ocelli" theory in various ways. He believes that the effect of light is due to the absorbed rays in the coloring matter of the cells and not to a mechanical action upon the protoplasmic membranes. He finds that the response depends not upon the intensity of the light,

but upon its quality, the more refrangible rays being the more active.

Radl, ('03), had previously proposed a theory of photic response in animals somewhat similar to that of Haberlandt in plants. He believed that orientation was a direct reaction to light pressure which, as he says, may resemble the pressure of an air-current.

Blaauw, ('09), by determining in photo-metric units the spectral regions, and calculating the energy values for each region from Langley's curve, attempted to explain the lack of harmony in the results of preceding investigators on the basis of energy distribution and of photo-chemical processes. From his experimental data on response of Avena and of Phycomyces in the spectral regions, he was able to construct curves consistent with those for visual sensitivity but with the maxima located in the blue and indigo.

Jennings, ('06), and Verworn, ('13), attribute response to a change in the physiologic state in the organism. The physiologic state depends upon metabolic processes which are influenced by external factors.

II. STATEMENT OF PROBLEM.

From a consideration of the literature cited, it is evident that the chief reason for the unsettled condition in regard to heliotropic response lies in the lack of accurate measurements of the quantity and quality of the light. The writer by carefully measuring and calibrating the quality and intensity of the light stimulus undertook the difficult task of correlating, if possible, the conflicting results and views held with reference to the nature of the light stimulus. This was attempted: (1) by a study of the response of Pilobolus to carefully calibrated light of different wave-lengths and intensities; and (2) by a determination of the energy relation, if any, between this light and heliotropic response.

III. MATERIALS AND METHODS.

To determine the relative energy values in the different spectral regions it was necessary to employ very delicate physical instruments capable of calibration in standard units. A thermopile and galvanometer constructed by Professor W. W. Coblentz of the U. S. Bureau of Standards, were used for this purpose. The thermopile was chosen because of its non-selective action in the different regions of the spectrum. The spectral regions used for experimental purposes were tested with a spectrometer from Adam Hilgar and Company, London, and the limits of the wave-lengths determined. Cultures of Pilobolus, grown under controlled conditions and kept for three hours in absolute darkness, were exposed to these measured spectral regions and the presentation time determined in each region. The threshold of stimulation thus found was taken as the measure of the sensitivity of Pilobolus to light of the different spectral regions.

The apparatus was of the type quite generally used in spectral experiments where artificial light is the source of illumination. Two light-tight compartments (a, Fig.1), each 270 x 30 x 30 cms., were placed as wings at angles of 120° to a middle compartment (b), 120 x 30 x 30 cms. The inside was blackened throughout with lamp-black and provided with screens (c) to shut off all lateral radiation. In each end of the apparatus was a metal box (d) with adjustable slit (e) in which the light source was enclosed. 154 cms. from the light source a lens (l) having a focal length of twenty-eight inches was

placed. Seventy-nine centimeters from each lens a carbon bisulphide prism (p) deflected a spectrum into the experimental chamber through adjustable slits in a screen (m). The thermopile (t) was connected in series with the galvanometer (g), and deflections of the galvanometer were read with telescope and scale at a distance of one meter. A tube (n), with the inside completely blackened, led from the thermopile to the Hefner lamp (h), and served to exclude all lateral radiation and draughts from the thermopile. This apparatus was located in a darkened basement room of the Natural History Building. The walls of this room were blackened and all lights used in connection with the apparatus were adjusted so that no stray rays could enter. The temperature and moisture conditions were comparatively constant. The room was thoroughly aired about two hours before each experiment.

The junctions of the thermopile were composed of bismuth and silver welded with tin and covered with platinum-black and lamp-black. When a ray of light falls upon this surface at the junction of the two metals it is absorbed as heat and transformed by the junctions into electro-motive force. A deflection of the galvanometer in series with the thermopile indicates the intensity of the radiation. The galvanometer used to indicate the energy absorbed has a moving astatic system suspended by a fine quartz fiber. It was shielded from magnetic disturbance by tubes of soft iron having small apertures through which the scale reflected by the suspended mirror could be read. Small

magnets placed near the galvanometer served to adjust its sensitiveness. The wires connecting the galvanometer to the thermopile were insulated and enclosed in a glass tube which in turn was covered with tin foil connected with the earth to prevent disturbances arising from slight variations of room temperature.

Much difficulty was to be anticipated in the manipulation and adjustment of instruments of such delicacy and precision. Although set up on a basement floor of heavy cement, the closing of doors in adjoining rooms or walking in the passage ways caused tremors that interfered with galvanometer readings. Street-cars passing a block away could be detected by a change in the sensitivity of the galvanometer. For these reasons the determinations were made at night and a time chosen when weather conditions were quiet and when very few people were working in the building.

The light sources used were a Nernst lamp of single glower type obtained from the Westinghouse-Nernst Company, and a 200-watt nitrogen filled tungsten Mazda made by the General Electric Company. Both were used on a 110-volt alternating current from the University power plant. The voltage was regulated by a volt rectifier and was remarkably constant. Each lamp was adjusted and carefully centered for the lens and prism. The lamp once adjusted remained fixed throughout a series of tests. In the Nernst lamp the glower, being one millimeter in diameter, served in the place of a narrow slit. A wide slit in front of the glower served to admit the direct light to the lens and to

cut off all lateral radiation. The light projected on the prism from the nitrogen-filled tungsten lamp was passed through a slit approximately three millimeters wide in front of the globe.

The spectral region admitted to the experimental chamber was sufficiently large to cover the slit of the thermopile. Each region used was admitted through a separate slit (2.5 x 10mm.) cut in the slides of a photographic plate-holder. The frame for these holders was permanently attached to the base of the apparatus and the slide corresponding to the region to be studied was inserted at the focus of the rays for this region. The thermopile, when measurements were in progress, was placed at ten centimeters from the slit.

The standard of light energy used was a Hefner lamp manufactured by Max Kohl and tested in the German Reichsanstadt. The conditions prescribed for its use were strictly followed and it was placed at two meters from the thermopile, the latter enclosed in the experimental chamber. The energy value of this Hefner lamp at two meters distant from the thermo-couple was determined in terms of the deflection of the galvanometer. The energy of the light from any of the spectral regions from the different light sources was similarly read, and expressed in terms of the Hefner lamp reading.

The mechanical value of radiation from the Hefner lamp burning under standard conditions as determined by Angstrom is $20.6 \times 10^{-8} \frac{\text{sec.cm.}^2}{\text{gr.cal.}}$ or about 8.3 ergs (Nichols,'05) per second per square centimeter at a distance of one meter (cf.Kniep &

Minder, '09). At two meters the radiation has one-fourth of this value, or 2.075 ergs. Accordingly, whatever the sensitiveness of the galvanometer, the deflection produced by the Hefner lamp under the given conditions is equivalent to 2.075 ergs. The energy values of the spectral regions used in the several experiments were measured and expressed as above indicated.

Since a galvanometer of the delicacy of the one used is subject to disturbances, its sensitivity was frequently tested and if necessary it was readjusted. To prevent the air from being vitiated by a too frequent use of the Hefner lamp, the red region of the spectrum of the Nernst lamp was repeatedly standardized in terms of the Hefner lamp and the energy of other regions in turn determined from this.

In the earlier work with the galvanometer the average of a series of ten deflections was taken in each spectral region. It was subsequently found that three or four readings would give practically the same result and, moreover, there was less chance for error arising from the change of magnetic and temperature conditions.

Since the energy values of the opposite ends of the spectrum are so widely different, the galvanometer was adjusted in its sensitivity (cf. Coblentz,'11) to the region in which the experiments were carried on. The values in every case, as shown in Table V, are expressed in terms of Hefner lamp values, and are directly comparable to each other. In the red, orange, and yellow, for example, the readings are taken with the galvanometer

at the same sensitivity as it was when the Hefner lamp readings were taken. The readings of the more refrangible and weaker regions were made with a more delicate adjustment of the galvanometer and compared with readings in the yellow, being finally expressed in terms of the Hefner lamp value.

Pilobolus.

Pilobolus is a well-known Mucor which grows abundantly upon manure. Coemans, ('59), Klein, ('72), Brefeld, ('81), and others have described its culture and mode of growth. The sporangiaphores late in the afternoon appear first at right angles to the substratum due to negative hydrotropism and later grow vertical due to negative geotropism (Pfeffer,'06). At this stage the sporangiaphores are extremely sensitive to light stimuli. In the evening the tips gradually grow into spherical yellow knobs and the sensitivity of the sporangiaphore is very much decreased, (Jolivette,'14). During the night the sporangiaphores become distended just below the yellow knobs and the characteristic transparent bulbs are formed. In the morning the matured sporangia are projected with considerable force.

A number of preliminary experiments were necessary to determine its behavior under the normal laboratory conditions. It was found that the rapidity of sporangial development bears a direct relation to the temperature. At 28° C. in the greenhouse sporangia are matured and projected early in the morning; at 20° C. they are ejected at noon; and at temperatures maintained below 8° C. they are matured and ejaculated after four days.

It was noted that in direct light there is a tendency to earlier bulb formation than in the shadow which is probably due to difference in transpiration (Leakon). Cultures which were well ventilated and kept in complete darkness developed sporangiaphores of the usual length and ejected the sporangia but little later in the day than those grown in the same green-house in the light.

Cultures kept in a laboratory where illuminating gas was used died out when windows were closed, (Crocker and Knight, '08). In this series of experiments special care was taken to work in rooms free of gas. Cultures of Pilobolus were grown in cases in the green-house at a relative humidity of 90%. They were transformed early in the afternoon to trays of moist sand and covered with earthen jars furnished with bent pipe ventilator tubes. Late in the afternoon a culture was taken from the tray and exposed for a definite period to a measured spectral region. During the exposure the culture rested on moist sand and was covered with a blackened shield to exclude stray light and to maintain the moisture conditions uniform. The moisture content of the air under the blackened shield as measured with Lambrechts' Polymeter ranged between 90 and 92% relative humidity. The culture after exposure was returned to the tray and covered with the ventilated jar. After one hour it was examined with a reading glass and the number of curved sporangiaphores recorded. Only cultures having sporangiaphores with pointed tips were used. Strict observance of the physiological state was found necessary,

since a culture with swollen tips exposed for three hours to the green rays failed to respond, while one with pointed tips responded in seventy minutes. The presentation time at the period of greatest sensitivity to stimuli was taken as the standard of measurement of the reaction of Pilobolus to light (Blaauw,'09).

IV. EXPERIMENTAL DATA AND RESULTS.

In Table II the measurements of wave-lengths as determined on a Hilger spectrometer for the Nernst and the nitrogen-filled tungsten Mazda lamps used in these experiments are given.

Table II.

Color	NERNST		TUNGSTEN	
	Included wave-lengths	Mean	Included wave-lengths	Mean
Red	7162 6185	667	7249 6915	708
Orange	6602 5639	612	6525 6098	631
Yellow	6795 5515	585	6038 5766	589
Green	5700 5100	540	5424 5033	523
Blue	5100 4816	496	4686 4591	464
Indigo	4793 4618	470	4423 4311	437
Violet	4300 4085	414	4081 3885	398

It will be noted that the mean of the wave-lengths of the regions indicated in the above table approximately coincide with the bright lines in the respective regions.

Table III gives the data for the galvanometer deflections for the Hefner lamp at a distance of two meters, and for the red region of the Nernst lamp. The energy value of the red region of the Nernst lamp was calculated from the Angstrom value of the Hefner.

Table III.

Light Source	Color	Wave-length	Galvanometer deflection in mm.	Average deflection in mm.	Ergs per sec. per cm.^{2}
Hefner lamp	Total radiation at 2 meters		540 - 70 = 470 530 - 90 = 440 510 - 70 = 440 520 - 70 = 450	450	2.075
Nernst lamp	Red	± 667	603 - 365 = 238 595 - 350 = 245 600 - 350 = 250 590 - 370 = 220	238	1.097

Table IV gives the scale readings for the spectral regions of the Nernst lamp with the values expressed in ergs as compared with the energy value of the red region taken from Table I. The galvanometer sensitivity was increased to get the determination for the violet and the calculation of the energy in the violet and the yellow made from that of the green previously determined.

Light Source	Color	Wave-lengths	Galvanometer deflection in mm.	Average deflection in mm.	Ergs per sec. per $cm.^2$
Nernst	Red	±687	445 - 155 = 290		
			470 - 195 = 275		
			470 - 210 = 260		
			495 - 235 = 260	271	1.097
	Orange	±612	445 - 345 = 100		
			440 - 360 = 80		
			485 - 400 = 85		
			465 - 375 = 90	85	.344
	Green	±540	352 - 315 = 37		
			373 - 338 = 35		
			403 - 369 = 34		
			453 - 409 = 44	37	.149
	Blue	±496	497 - 475 = 22		
			523 - 500 = 23		
			540 - 526 = 20		
			554 - 524 = 30	24	.097
	Indigo	±470	448 - 430 = 18		
			468 - 445 = 23		
			490 - 475 = 15		
			540 - 522 = 18	19	.077
			Galvanometer sensitivity raised to get reading on violet		
	Green	±540	290 - 235 = 55		
			300 - 250 = 50		
			335 - 295 = 40		
			345 - 305 = 40	46	.149
	Yellow	±585	410 - 420 = 90		
			410 - 315 = 95		
			415 - 320 = 95		
			420 - 335 = 85	91	.295
	Violet	±414	340 - 355 = 15		
			318 - 330 = 12		
			325 - 340 = 15		
			327 - 336 = 9	12	.038

Table V gives the galvanometer deflections in the spectral regions of the 200-watt nitrogen-filled tungsten Mazda lamp as compared with those of the Hefner, - the values being expressed in ergs. Since the spectrum of the tungsten lamp was but 8 mm. in width and the slit of the thermopile 18 mm., a correction was necessary in order to make the readings comparable with those of the wider spectral regions of the Nernst lamp. The calculations for the energy in the more refrangible regions was made from the value of the yellow.

Table V.

Light Source	Color	Spectral region	Galvanometer deflection in mm.	Average corrected deflections in mm.	Ergs per sec. per cm.^{2}
Hefner	Total radiation		480 - 370 = 110		
			485 - 360 = 125		
			490 - 370 = 120		
			500 - 385 = 115	117	2.075
Tungsten	Red	$\pm$708	550 - 350 = 200		
			545 - 345 = 200		
			540 - 340 = 200		
			540 - 340 = 200		
			200 x 9/4 =	450	7.98
	Orange	$\pm$631	520 - 420 = 100		
			527 - 425 = 100		
			535 - 440 = 115		
			552 - 452 = 100		
			104 x 9/4 =	234	4.15
	Yellow	$\pm$589	504 - 440 = 64		
			512 - 450 = 62		
			522 - 460 = 62		
			522 - 461 = 63		
			62 x 9/4 =	140	2.48
	Galvanometer changed to higher sensitivity				
	Yellow	$\pm$589	400 - 230 = 170		
			405 - 240 = 165		
			425 - 260 = 165		
			435 - 260 - 175		
			169 x 9/4 =	378	2.48
	Green	$\pm$523	310 - 225 = 55		
			395 - 315 = 80		
			420 - 345 = 75		
			440 - 365 = 75		
			71 x 9/4 =	162	1.053
	Blue	$\pm$464	315 - 278 = 37		
			328 - 290 = 38		
			410 - 372 = 38		
			385 - 340 = 45		
			39.2 x 9/4 =	89	.578
	Indigo	$\pm$437	210 - 185 = 25		
			210 - 185 = 25		
			250 - 228 = 22		
			250 - 220 = 30		
			25 x 9/4 =	56	.364

Table V. (Continued)

Light Source	Color	Spectral region	Galvanometer deflection in mm.	Average corrected deflections in mm.	Ergs per sec. per $cm.^2$
Tungsten	Violet	± 398	440 - 332 = 8		
			488 - 478 = 10		
			508 - 498 = 10		
			508 - 499 = 9		
			9 x 9/4	= 20	.130

Tables VI and VII give the data for the determination of the presentation periods of Pilobolus in the different spectral regions. It was not deemed necessary to repeat here the periods of exposure longer and shorter than the ones which gave the final decisive results.

Table VI.

Light Source	Series Number	Color	Wave-length	Temp. degree C.	Time of exposure in minutes	Per cent positive	Per cent indifferent	Presentation time in min.
Nernst	R_{11}	Red	± 667	24.3°	6:13 p.m. - 7:28 p.m. = 75	0	100	
	R_{12}	"	"	25.7	4:05 p.m. - 5.25 p.m. = 76	88	12	
	R_{13}	"	"	24.0	4:04 p.m. - 6.21 p.m. = 77	100	0	76
	O_{13}	Orange	± 612	26.3	5:56 p.m. - 7:08 p.m. = 72	0	100	
	O_{16}	"	"	24.5	4:18 p.m. - 5:33 p.m. = 75	100	0	
	O_{17}	"	"	24.7	7:56 p.m. - 9:09 p.m. = 73	52	48	73
	Y_{19}	Yellow	± 585	24.8	7:55 p.m. - 9:05 p.m. = 70	0	100	
	Y_{20}	"	"		6:01 p.m. - 7:15 p.m. = 74	100	0	
	Y_{26}	"	"	24.4	7:06 p.m. - 8:18 p.m. = 72	50	50	72
	G_{8}	Green	± 540	24.6	7:50 p.m. - 9:00 p.m. = 70	100	0	
	G_{10}	"	"	26.8	6:51 p.m. - 7:56 p.m. = 65	0	100	
	G_{11}	"	"	24.3	5:34 p.m. - 6:42 p.m. = 68	33	66	69
	B_{10}	Blue	± 496	23.6	7:40 p.m. - 8:40 p.m. = 60	0	100	
	B_{17}	"	"	23.7	8:15 p.m. - 9:22 p.m. = 67	90	10	
	B_{19}	"	"	24.8	5:41 p.m. - 6:46 p.m. = 65	66	34	65
	I_{12}	Indigo	± 470	26.0	5:00 p.m. - 6:05 p.m. = 65	75	25	
	I_{13}	"	"	26.0	6:58 p.m. - 8:00 p.m. = 62	25	75	
	I_{16}	"	"	24.7	6:48 p.m. - 7:51 p.m. = 63	20	80	63
	V_{10}	Violet	± 414	25.7	4:58 p.m. - 5:50 p.m. = 52	25	75	
	V_{11}	"	"	24.3	4:21 p.m. - 5:19 p.m. = 58	75	25	
	V_{13}	"	"	25.2	6:49 p.m. - 7:44 p.m. = 55	60	40	55

Table VII.

Light Source	Series Number	Color	Wave-length	Temp. degree C.	Time of exposure in minutes	Per cent positive	Per cent indifferent	Presentation time in min.
Tungsten	R_{T2}	Red	±708	26.6	6:32 p.m. - 7:37 p.m. = 65	0	100	
	R_{T3}	"	"	24.0	6:39 p.m. - 7:47 p.m. = 68	50	50	
	R_{T4}	"	"	26.4	4:27 p.m. - 5:36 p.m. = 69	71	29	68
	O_{T3}	Orange	±631	26.8	5:43 p.m. - 6:43 p.m. = 60	95	5	
	O_{T4}	"	"	26.8	6:45 p.m. - 7:40 p.m. = 55	23	77	
	O_{T5}	"	"	24.3	5:38 p.m. - 6:34 p.m. = 56	87	15	56
	Y_{T4}	Yellow	±589	23.6	6:00 p.m. - 7:01 p.m. = 61	0	100	
	Y_{T8}	"	"	25.0	6:05 p.m. - 7:09 p.m. = 64	75	25	
	Y_{T9}	"	"	24.4	7:11 p.m. - 8:14 p.m. = 63	75	25	63
	G_{T5}	Green	±523	26.3	4:36 p.m. - 5:41 p.m. = 66	87	13	
	G_{T3}	"	"	26.0	6:54 p.m. - 7:57 p.m. = 63	71	29	
	G_{T8}	"	"	24.6	5:44 p.m. - 6:44 p.m. = 60	82	18	59
	B_{T6}	Blue	±464	24.3	5:45 p.m. - 6:43 p.m. = 58	66	33	
	B_{T7}	"	"	24.8	4:38 p.m. - 5:33 p.m. = 55	60	40	
	B_{T8}	"	"	25.2	6:45 p.m. - 7:35 p.m. = 50	25	75	55
	I_{T3}	Indigo	±437	24.9	6:34 p.m. - 7:24 p.m. = 50	0	100	
	I_{T9}	"	"	25.2	7:08 p.m. - 8:03 p.m. = 55	32	68	
	I_{T10}	"	"	24.0	4:45 p.m. - 5:42 p.m. = 57	84	16	53
	V_{T12}	Violet	±398	25.2	3:59 p.m. - 4:58 p.m. = 59	100	0	
	V_{T13}	"	"	23.5	5:05 p.m. - 5:57 p.m. = 52	25	75	
	V_{T14}	"	"	23.8	5:37 p.m. - 6:27 p.m. = 50	33	66	50

In Plate II the spectral energy curves for the Nernst and for the tungsten lights represent in graphic form the data recorded in Tables II, IV and V. Wave frequencies of light are represented by the abscissae and the mechanical energy in ergs per second by the ordinates. The spectral energy for the tungsten lamp is plotted on a scale having ten times the value of that used for the energy of the Nernst lamp. A comparison of the above curves with those of Coblentz, ('11), for the Nernst and the tungsten lights, and those of Moll, ('07), for the Nernst light will show that a higher value was obtained in the violet. Although repeated attempts were made to bring these results in the violet into conformity with those of Coblentz and Moll, they were not successful. The difference may be in part due to the use of the Nernst lamp with the globe removed.

A number of investigators have maintained that the response of organisms to light of different nature may be correlated with energy equivalence. Pilobolus, exposed to the spectral regions of the Nernst and tungsten lamps differing rather widely in energy, will respond as indicated in Plate III. In plotting these graphs the wave-lengths and frequencies are disregarded. The abscissae represent the presentation time and the ordinates the energy of the region expressed in ergs, the data being taken from Tables IV, V, VI and VII.

An inspection in Plate III shows that an actual decrease in the rate of response takes place with increase of the photic energy. This shows, conclusively, there is no direct relation

between response and the energy of the different regions. Thus, the lens theory of Haberlandt, ('05), and the orientation theory of Radl, ('03), that response is due to a pressure that the light exerts on the cells of the organ are not applicable to the response of Pilobolus.

Likewise, a statement in Blaauw's theory of response, ('09, p. 30), namely, that the plant perceives only the quantity of energy as a stimulus, can not be taken literally, for he says,- "Fur diesen constanten Effekt ist eine konstante Quantitat Energie notig und es ist also fur die Pflanze gleichgultig, wie diese Energie, uber Leit und Intensitat verteilt, zugefuhrt wird. Die Pflanze empfindet nur die Quantitat Energie als Reiz; die Leit und die Intensitat sind nichts mehr als Faktoren von der Energiemasse. Nur diese Quantitat Energie wirkt als Reiz, fue die Pflanze selbst besteht weder die Intensitat, noch die Leit als eine absonderliche Grosse."

A superficial study of these curves, however, might lead one to the erroneous belief that increase of energy has an inhibiting effect on the tropic response. If this were true, the decrease in the irritability in the tungsten light toward the higher energy values would be much more rapid than in those of the Nernst. Further discussion of the energy relation will be taken up later.

If the presentation periods be plotted in reference to frequency of the light waves in the spectral regions to which Pilobolus was exposed, the results will appear as in Plate IV.

These graphs are based on the data given in Tables II, VI and VII. In this instance it will be noted that response in Pilobolus takes place in every region of the spectrum, and that the presentation period decreases from red to violet, or conversely, that the irritability increases from red to violet. These results then confirm those obtained by Brefeld, ('81, p. 60), and Graentz, ('98), and are contrary to those of Sorokin, ('74) and of Fischer von Waldheim, ('75).

With one exception in the orange,- due possibly to instrumental difficulty,- the graphs as given on Plate IV are remarkably constant in their gradual increase from red to violet. At no time was there found in this series of experiments any intermediate minimum such as Wiesner obtained in yellow, ('79), and Dandeno in green, ('03), nor a maximum as reported by Guillemin, ('57), in the violet and in the red, by Dandeno in yellow, and by Blaauw, ('09), in indigo. The sudden increase in irritability noted in the orange of the tungsten is, in my opinion, not to be considered a maximum since the regions on either side of this fall into the general trend of the graph. While it is possible that this high value in the orange is due to some selective action on the part of the plant, it seems more probable that there was a reflection in the prism which escaped detection in the spectrometer.

The slope of the graphs from the violet toward the red shows that the response of the organism has a very marked relation to wave frequency. Calculation of this relation shows that the

product of the square root of the frequencies and the presentation time is so nearly uniform as to warrant attention later. (Cf. Nernst, '99; Verworn, '13.) The results of this calculation are given in Table VIII.

Attention must be called to the fact that the graphs representing the time and frequency relation (Plate IV) of Pilobolus for the two sources of light (Nernst and tungsten) are not nearly identical as would be the case were wave-frequencies alone responsible for the differences in the induction periods. Furthermore, the two graphs diverge somewhat from the violet toward the red giving additional evidence that energy is a factor in the relative time required for phototropic excitation. The fact that energy does play a part in response is further manifest from the results given in Table VIII. This table shows that while the square roots of the frequencies constitute an ascending series, the presentation periods times the square roots of the frequencies form a descending series. It should also be noted that the constant for the Nernst is considerably larger than that for the tungsten.

Table VIII.

Light Source	Color	Wave-length	Fre-quency	Sq.root of frequency	Presentation time in min.	Sq.root of frequency X time = const.
Nernst	Red	±667	450	21.2	76	1611
	Orange	±612	494	22.2	73	1620
	Yellow	±585	512	22.6	72	1627
	Green	±540	556	23.6	69	1628
	Blue	±496	607	24.6	65	1599
	Indigo	±470	638	25.2	63	1587
	Violet	±414	738	27.1	56	1517
Tungsten	Red	±708	424	20.6	68	1400
	Orange	±631	472	21.7	56	1215
	Yellow	±589	509	22.5	63	1417
	Green	±523	574	23.9	59	1410
	Blue	±464	648	25.4	55	1397
	Indigo	±437	686	26.3	53	1393
	Violet	±398	753	27.4	50	1370

Since the time of response of Pilobolus to the light of the tungsten and Nernst lamps, respectively, is by no means in direct proportion to their spectral energy values, and since there is found to exist some relation of the energy to the time of response, the question arises as to the possibility of expressing this relation in simple mathematical terms.

Wiesner, ('79), has shown that the excitation of the plant increases less rapidly than the photic stimulus which produces it.

Pfeffer, ('83), through the study of the reaction of swarm spores and bacteria to chemical stimuli established the application of the Weber-Fechner law to plants. This law states that whereas the intensity of the stimulus increases in geometrical progression the intensity of the reaction increases in arithmetical progression, or that response varies with the logarithm of the stimulus. This is expressed in the formula,-

$S_1 - S_2 = A \log \frac{I_1}{I_2}$, where S_1 and S_2 are the sensations, I_1 and I_2 the respective intensities of the stimuli, and A is a constant which varies with the quality of the stimulus.

This law which was developed from a psycho-physical basis by Weber and Fechner, ('82), was later shown by Muller, ('78), to have a physiological significance. While Pfeffer showed its application to chemotropic stimuli, he expressed a belief that it would be found true in other forms of reaction, such as phototropism and geotropism.

Massart, ('88), has shown that the irritability of the

sporangiaphores Phycomyces between two unequal intensities of light follow the Weber-Fechner law in their reaction.

If for the term "sensation", which belongs to the realm of psychology, we substitute "irritability" (cf. Preyer, '74), the Weber-Fechner law may be tested in its application to the present problem within the limits of the measured intensities of the spectral regions of the two light sources. It will be noted that an approximation only, is possible because of the necessity for interpolation of values to bring the comparable measurements within the same spectral region. In Table IX are given the measured and interpolated values of the energy and the presentation time, together with the solution of the formula to obtain the value of constant "A" for each given region. The value of "A", however, is seen to decrease rather uniformly through the spectral regions and this strengthens the belief already expressed, namely, that the two factors, wave-frequency and energy combined, give the phototropic response. If the value of "A" in each case is multiplied by the wave-frequency of the region in which the measurements were made, an approximation to a general constant for the whole visible spectral region is obtained as shown in the last column of Table IX. It is desired that further work be done in this line to test this law more thoroughly.

Table IX.

Frequency of light wave (sec.)	Work in Ergs		Presentation Time		$\log_{10} I_n$	$\log_{10} I_t$	$-\log_{10} \frac{I_n}{I_t}$	$S_n - S_t$	$-A$	$-A \cdot f$
	I_n	I_t	S_n	S_t						
424	(1.660)	7.980	(77.8)	68	0.2201	0.9020	0.6819	9.8	14.3	6060
450	1.097	(5.720)	76	(66.5)	0.0402	0.7574	0.7172	9.5	13.2	5930
472	(.650)	4.150	(74.5)	56	$\bar{1}.8129$	0.6180	0.8051	8.5	11.55	5460
494	.344	(3.050)	73	(63.8)	$\bar{1}.5366$	0.4843	0.9477	9.2	9.75	4820
509	(.303)	2.48	(72.2)	63	$\bar{1}.4814$	0.3945	0.9131	9.2	10.1	5130
512	.295	(2.36)	72	(62.8)	$\bar{1}.4698$	0.3729	0.9131	9.2	10.2	5220
556	.149	(1.34)	69	(60)	$\bar{1}.1732$	0.1271	0.9539	9.0	9.43	5240
574	(.126)	1.053	(67.6)	59	$\bar{1}.1004$	0.0224	1.0220	8.6	8.46	4950
607	.097	(.750)	65	(57.2)	$\bar{2}.9868$	$\bar{1}.8751$	0.8883	8.2	9.12	5540
638	.077	(.660)	63	(55.5)	$\bar{2}.8865$	$\bar{1}.8195$	0.9330	7.5	8.04	5130
648	(.072)	.578	(62.3)	55	$\bar{2}.8573$	$\bar{1}.7619$	0.9046	6.8	7.53	4880
686	(.055)	.364	(59.6)	53	$\bar{2}.7404$	$\bar{1}.5611$	0.8207	6.6	7.98	5460
738	.038	(.160)	56	(50.7)	$\bar{2}.5798$	$\bar{1}.2041$	0.6243	5.3	8.50	6280
753	(.032)	(.130)	(55)	50	$\bar{2}.5052$	$\bar{1}.1139$	0.6087	5.0	8.23	6200

V. CONCLUSIONS AND THEORETICAL DISCUSSION.

In considering the lack of conformity in the results of the investigations in the field of phototropism it must be remembered that the plant is an organism existing in a physiological state continuously changing with the varied physical and chemical factors of its environment. A slight change in some one of the factors may markedly change the relation of the organism to every other factor (cf. Verworn, '13). Attention has already been called to the disturbing influence of the slightest trace of illuminating gas in the laboratory air upon Pilobolus. The researches of Crocker and Knight, ('08), have shown its vitiating influence upon the higher plants. A review of many articles upon phototropism shows that illuminating gas has furnished the source of light for the experimental work. Thus Wiesner, ('79), Figdor, ('93), and Blaauw, ('09), in order to subject the plant to different intensities of light varied the distance from the gas-flame from a few centimeters to several meters. Even though the presence of the gas in the room was not destructive to the plants used by these investigators, one might see from later work (Richter, '06, Crocker and Knight, '08) the inhibiting effect that mere traces of the gas, or the products of combustion, has upon the sensitivity. The presence of these deleterious agents unquestionably affect in degrees according to the distance of removal from the burner the physiolcgical condition of the plants and thereby a change in their irritability. The above objections naturally do not affect those experiments of Wiesner, Figdor and Blaauw, where the sun or arc lights were used.

A noticeable difference between the results of the present series of experiments and those of earlier workers lies in the absence of the maximal and minimal points of response in the spectrum. Inquiry into the cause for this difference naturally leads first to the study of the nature of the light obtained from different sources.

The theory of light as formulated by Maxwell and accepted by physicists of the present time states that light consists of short electro-magnetic waves which are produced by violent agitation of particles either from the electric current or other source of heat. Every source of light used for illumination has its own characteristic spectrum which differs from that of every other source, and the energy of radiation of each wave-length derived from one source differs from that of the corresponding wave-langth from every other source (Nutting, pp. 12 and 197; Fery, '08; Coblents, '11). Moreover, the spectrum from any given source changes according as the absolute temperature of the source is increased. The maximal spectral energy is found to move toward the violet end with a rise in the absolute temperature. (Ives, '10, Drysdale, '08, Nichols, '03, Wien, '93). Thus we find that bodies heated to 500° C. emit only red rays in the visible spectrum, while the sun at a probable temperature of 6000° C. emits the greatest amount of energy in the violet. (Cf. Duff, p. 455).

The Nernst and the tungsten lamps heated to about 2300° C. (Hyde) show the spectral energy to increase from the ultra-

violet to a maximum in the infra-red. (Moll, '07, Coblents, '11). Since we find the energy highest in the red of the visible spectrum we should expect from the discussion already given that in the response of Pilobolus, the slowness of the waves in the red region is in a measure compensated by their greater energy. The frequency having a much more noticeable effect than the energy values of the waves in the response of Pilobolus, Table IX, Plates III and IV, may more than compensate for the lack of energy in this region. The regions between the red and violet having a gradual decrease in energy and an increase in frequency produce a response intermediate in time between that of the red and the violet. From the physical basis one could then predict the first maximum in ultra-violet and a second maximum in the orange in the response of plants exposed to a light having its maximum spectral energy in the orange, as the energy of this region would more than compensate for the slowness of the waves and a second maximum thus appear.

The results obtained by Guillemin, ('57), who by the use of different prisms was able to obtain spectra from the sun in which the relative intensity varied for the same wave-length, substantiate this view. With a rock-salt prism which transmits dark heat rays, he obtained the first maximum in the ultra-violet and a second maximum in the ultra-red; with a quartz prism which transmits the chemical rays, he obtained the first maximum in the violet and a second between the red and infra-red; with a flint-glass which best transmits the intermediate rays, he obtained the first maximum in the violet and a second in the green.

He further found that the second maximum advanced more and more into the visible spectrum as the water vapor in the air was increased and the position of the sun approached the horizon.

Wiesner's results with seedlings in the sun's spectrum may in a measure be correlated with this line of thought. Due to the vapor, etc., present in the atmosphere the maximum energy of the sun's spectrum at noon is usually near the yellow (Langley, '83, p. 33). The use of a bi-convex lens would so focus these rays as to bring the intensity in the yellow to a very high value which may be responsible for the indifferent, or even negative heliotropic response. (Oltmanns, '92). His results show a very regular decrease in the presentation time from the green into the ultra-violet, and bring the maximum irritability into the ultra-violet region. This would naturally follow from the increasing frequency and very considerable energy of this region in the same manner, as determined and recorded in this paper, (Table IX).

In Blauuw's experiments, ('09), because of the higher absolute temperatures of the light sources - sun and arc-lamp - the maximum energy is near the yellow. He obtained no response in the red end beyond the yellow-orange. In the indigo with a higher frequency and lower energy value he found a maximum response. This again accords beautifully with the results already described in this paper.

Divergent views held by previous investigators regarding the region of maximum response in the spectrum can be readily

explained on the basis of energy value and frequency. That this has not previously been done is largely to be attributed to the difficulty encountered in determining the spectral values. Thus, Gardner, ('44), observed that the intensity of light had only a subordinate influence. Sachs, ('67), and Loeb, ('06), state that the shorter waves are the more active and that the reaction is proportional to the intensity. Towle, '00), says of Cypredopsis that the response is shorter in the stronger light "though the difference is too slight to warrant one in drawing any inferences from it". Allen and Jolivette ('13, p. 581) concluded from their experiments where colored glass screens were used that "the light of short wave-length has no preponderating influence at least in determining the phototropic reactions of Pilobolus". It is noted in the experiment upon which this conclusion is based that the blue rays are balanced against the sum total of all the rays included in white light. From the relatively greater influence which the preceding pages of this paper have shown the frequency of light to exert upon Pilobolus as compared to that of intensity, this conclusion from unmeasured quantities of light could be anticipated.

In a later paper, however, Miss Jolivette ('14, p. 119) using different kinds of light sources states, "Pilobolus fires its sporangia in larger numbers toward the lights in which the blue rays are greatest. In other words, it is more responsive to activic rays. The intensities in the different wave-lengths are not measurable". She further says that the energy given

off by the source of light apparently does not compare in effect with the distribution of the same in different portions of the spectrum. In the experiments using a 16-candle-power tungsten and a 32-candle-power carbon filament lamp the large majority of the sporangia went to the tungsten light although its total energy was but half that of the carbon. From this she concludes that the differences in distribution in the spectrum outweigh in effect the differences in the total energy of the two sources, a qualitative conclusion which the present paper through quantitative methods has shown to be valid.

Summary

1. Pilobolus responds to the light of all the regions of the visible spectrum.

2. The presentation time decreases gradually from red to violet. There is no indication of intermediate maxima or minima.

3. The presentation time does not vary in direct ratio with the measured value of the energy of the light in the different regions of the spectrum.

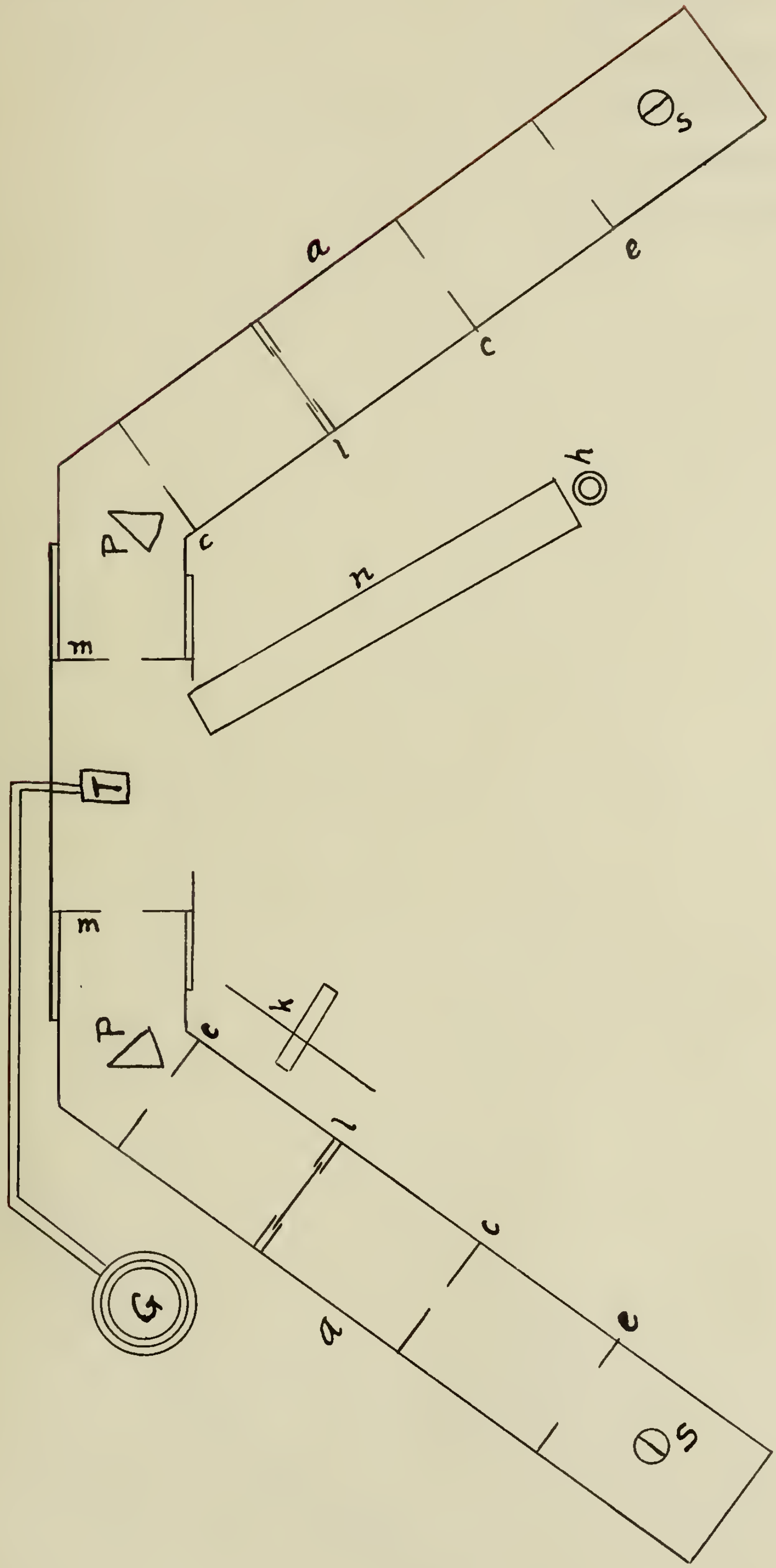
4. The presentation time varies in inverse ratio to the square roots of the wave frequency.

5. The product of the square root of the frequency times the presentation time decreases with the decrease in the energy value of the spectral regions, and is an approximate constant for a given light-source.

6. The spectral energy in its relation to the presenta-

tion time may be expressed approximately in the Weber-Fechner formula, if the wave-frequencies be made a function of the constant.

PLATE I.



General Plan of Apparatus

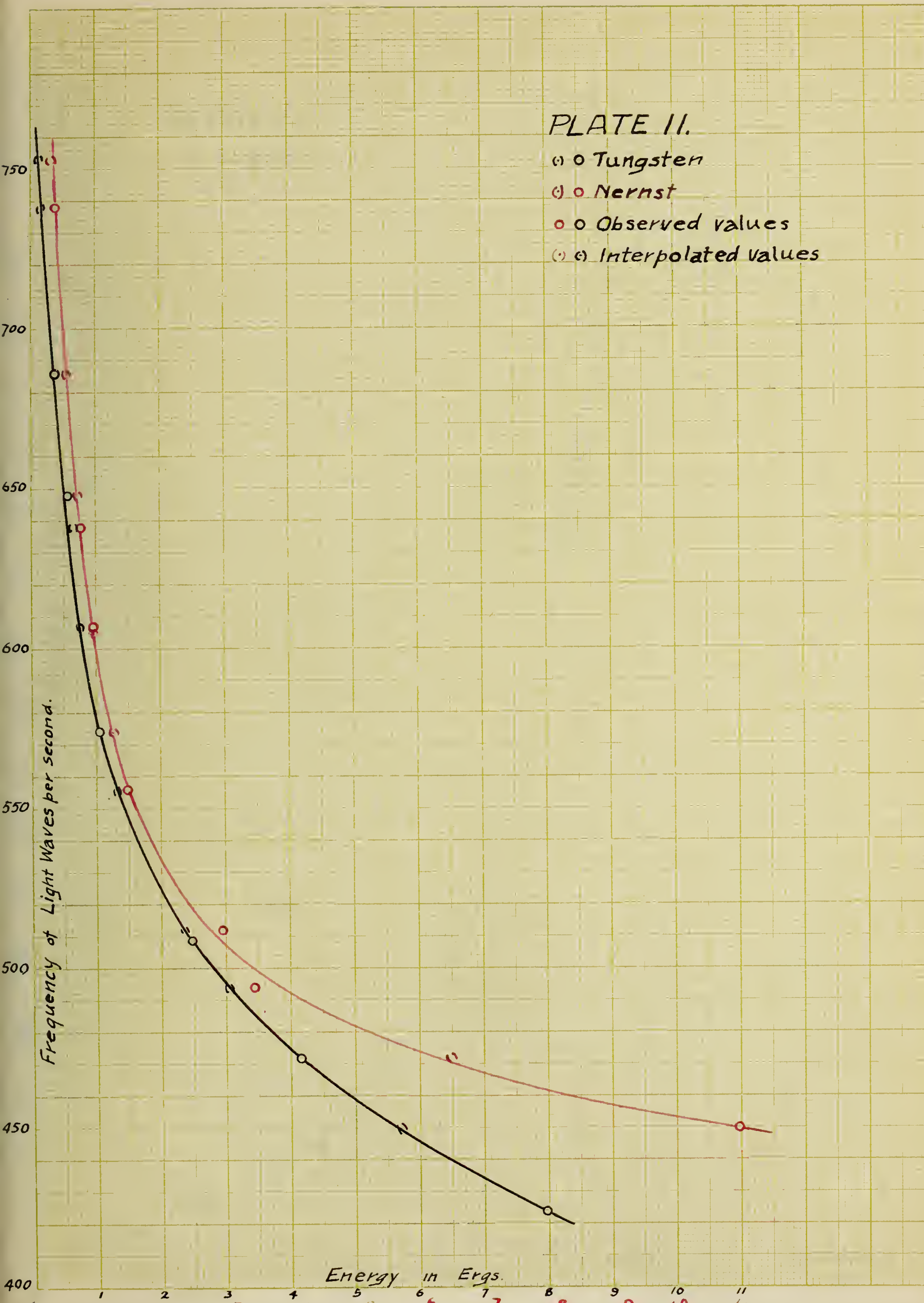


PLATE II.
Tungsten
Nernst
Observed values
Interpolated values
Frequency of Light Waves per second.
Energy in Ergs.
750
700
650
600
550
500
450
400
1 2 3 4 5 6 7 8 9 10 11
.1 .2 .3 .4 .5 .6 .7 .8 .9 1.0 1.1

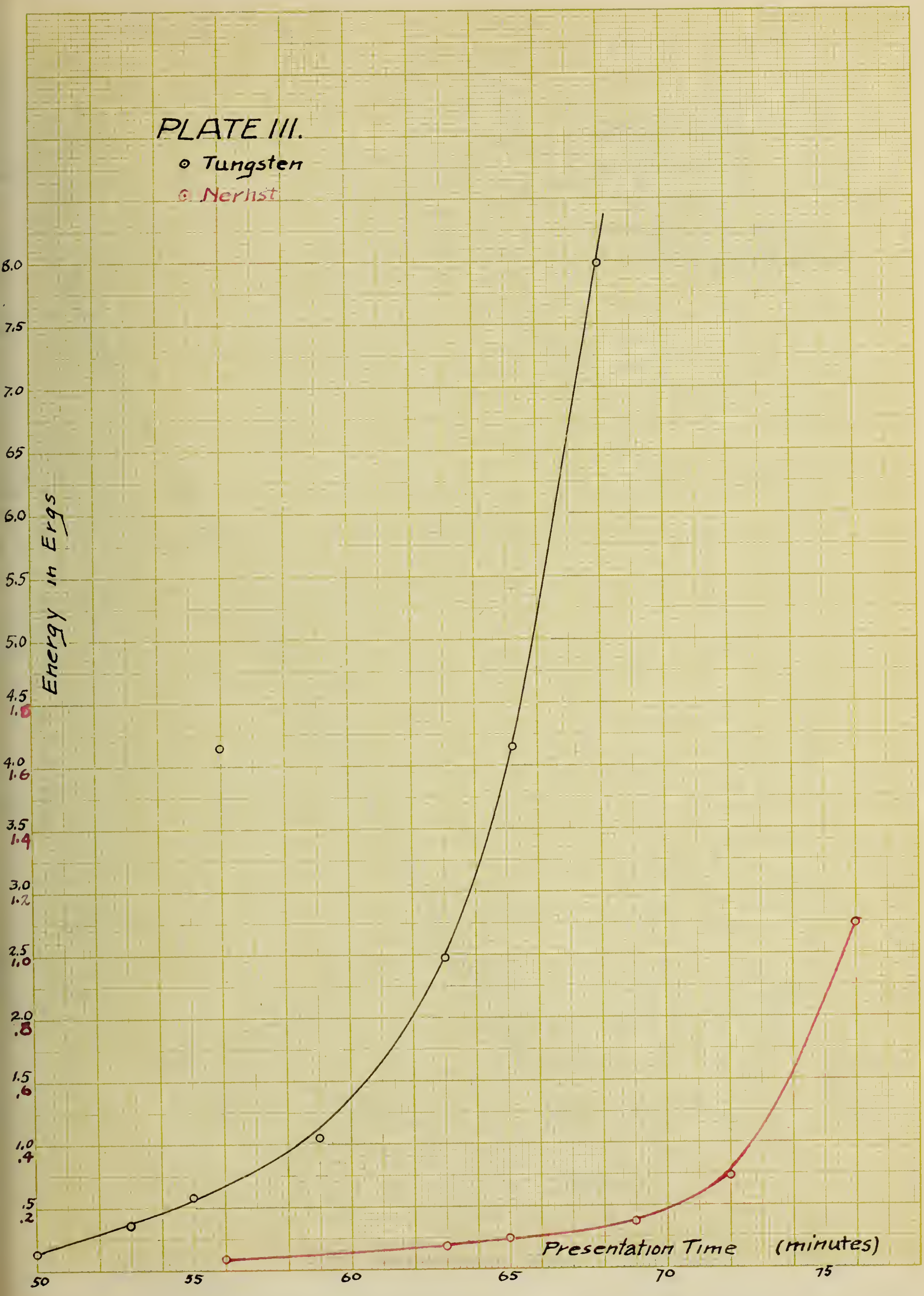


PLATE III.
Tungsten
Nerhst
Energy in Ergs
Presentation Time (minutes)
8.0
7.5
7.0
65
6.0
5.5
5.0
4.5
1.8
4.0
1.6
3.5
1.4
3.0
1.2
2.5
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.5
.2
50
55
60
65
70
75

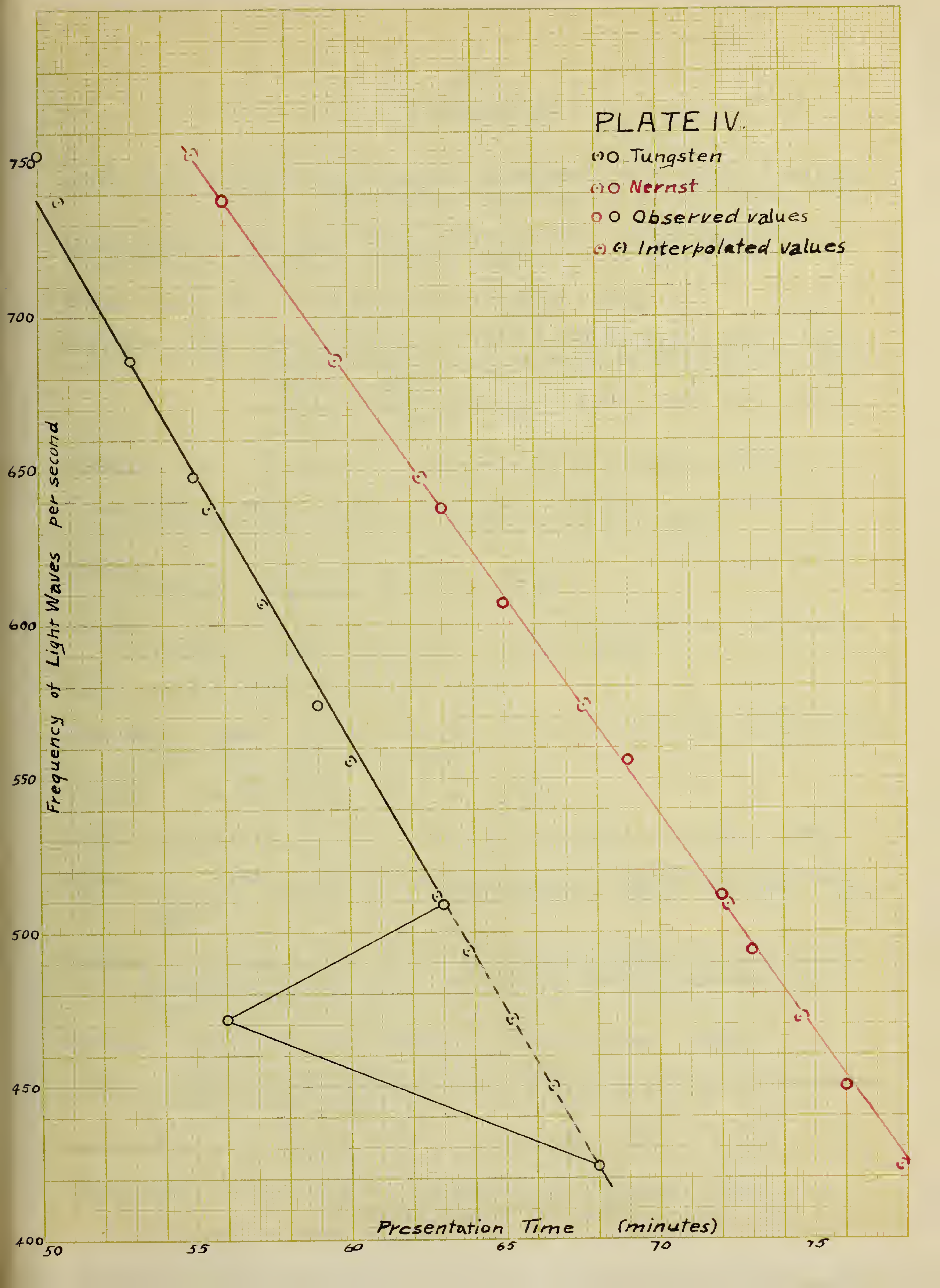
PLATE IV.
Tungsten
Nernst
Observed values
Interpolated values
Frequency of Light Waves per second
750
700
650
600
550
500
450
400
50
55
60
65
70
75
Presentation Time (minutes)

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